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The relation of the health of the host and other factors to infection of Apium graveolens by Septoria Apii

H. E. THOMAS

Students of immunity and susceptibility have been slow to recognize any fundamental distinctions in the relations of host and parasite in the great group of organisms which cause disease in plants and animals and yet the concepts of saprophyte, semi-saprophyte, and obligate parasite have been current at least since the time of DeBary. Under the influence perhaps chiefly of Ehrlich's side chain theory of immunity, degrees of resistance have been regarded on the one hand as inversely parallel to the virulence of the attacking organism and on the other hand as directly parallel to the vigor of the host. In plant pathology this view has been particularly prominent in the literature of the facultative parasites. With the development of the science of immunity, the animal pathologist has gone so far as to regard the interactions of host and parasite as specific in each case. It is becoming increasingly apparent that the specificity in the relation of plant pathogens with their hosts must be reckoned with. The saprophytic fungus may be able to live on dead tissue from a wide range of plants, sometimes showing little preference for any one of them. The semisaprophyte may or may not be more limited in its food range on dead material and attacks from one to a considerable number of living plants with varying degrees of virulence and with variable results to the hosts. The obligate parasite is usually still more restricted in its host range and is much more closely

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adapted to the living host, having completely lost the ability to grow on dead tissue even that of its most common host. In the more highly specialized forms, the relation may become specific to such a degree that a comparatively slight change in either host or fungus will completely change the virulence of the parasite or the effect on the host. It is to be expected, after the long period of association necessary for the close adaptation of fungus to host, that both would be more or less similarly influenced by their environmental conditions. I shall present data to show that the infection of *Apium graveolens* by *Septoria Apii* is favored by conditions which accelerate the growth of the host.

HISTOCICAL INTRODUCTION

The late blight of celery was first reported in the United States in 1891 by Chester (4) and Humphrey (15). It had been described the previous year from Italy by Briosi and Cavara (3), probably the earliest record of the disease. Prillieux and Delacroix (29) reported it in France in 1894, and Sorauer (35) recorded its occurrence in Germany in severe form in 1896. It came to the notice of Salmon (34) in England about 1906. By 1897 the disease in America had spread to California and was reported by Rogers (31) as a serious pest in that state. An interesting suggestion as to the possible source of origin of the disease on cultivated celery comes from Pethybridge (26). This author found on wild celery a fungus which appeared to be identical with the form on the cultivated crop. He was able to transfer it to cultivated celery and produce typical infection. The wild form was growing in comparatively complete isolation and Pethybridge believes it very unlikely that the fungus could have spread from cultivated plants to this host. Hence he concludes that the wild form is probably the source of the pest. Dorogin (9) in Russia reports a new species of *Septoria* on celery, *S. Apii graveolentis*, in addition to the common species. The former is said to be more destructive than the latter. During the early and middle parts of the growing season no severe infection of celery is usually noted, although Salmon (34) found that serious damage was done throughout the growing season. Further study of the relation of this disease to temperature and other seasonal conditions is needed.

Duggar and Bailey (10), Clinton (5 p. 267), and Link and Gardner (19) have observed that both celery and celeriac are attacked by *Septoria* in storage. The first authors noted that over 50 per cent of the stored crop was made unsalable by this fungus in one instance.

No extensive observations seem to have been made on the degree of susceptibility of the commercial varieties of celery to the late blight. Salmon (4) tested several varieties and arranged them in the following series, the first being most susceptible: Solid White, Clark's Early Market, Superb Pink, Giant Red, Standard Bearer, celeriac. Howitt (4) noted that Golden Self Blanching was particularly susceptible. White (42) concluded in general that Golden Self Blanching was very susceptible to disease while Henderson's Easy Blanching was comparatively free from disease. On wild celery Pethybridge (26) found fewer and smaller spots produced by *Septoria*, which seemed never to kill the leaf entirely. He states that the fungus occurs on parsley though rarely in the British Isles. Cooke (7) and others have considered the forms on celery and parsley identical, although I have found no record of the transfer of the *Septoria* from one of these hosts to the others.

Some interesting observations were made by Kinney (16) on the relation of cultural practice to blights of celery. He found that the amount of disease was reduced by mulching with seaweed, soil, coarse manure or even blighted leaves. Plants grown in the shade of trees seemed to be less subject to "blight." Unfortunately the author did not distinguish between *Septoria* and *Corcospora* blight. Zobel (43) believes that reduction of the amount of manure in the trenches and top dressing the soil with kainit greatly reduced the amount of *Septoria* in England.

Attempts to avoid or control the late blight, while not uniformly successful, are in practical agreement in the essentials. Rogers (31), Salmon (34), Howitt (14), Coons and Levin (8), and Krout (18) obtained practical control of the disease with Bordeaux mixture.

MATERIALS AND METHODS

I have attacked the problem of the relation of health, age and other conditions to susceptibility by means of inoculation experi-

ments with celery in the greenhouse, where the health of the host was altered by various experimentally controlled conditions. Each set of plants was accompanied by control plants and no attempt has been made to compare in any detail plants inoculated at different dates or plants which for any reason cannot be referred to the same control plants. Some experiments with hosts other than celery were made to show the host range of the *Septoria* and will be taken up in detail later in the paper. The plants were grown in pots usually in garden oil which was screened and mixed to obtain uniformity. Inoculations were made by atomizing with a suspension of spores taken from infected leaves. The plants of a series were placed in a group, alternating test and control plants, and were atomized from above and from the sides to obtain maximum dosage. The spore suspension was diluted in one case 1 to 10 and in another 1 to 20 without any marked decrease in the amount of infection produced. The counts in these cases were not high, however. The inoculation chamber was a rectangular box constructed from window sashes and lined with burlap which was saturated with water at the time of inoculation. The plants were usually kept in the inoculation chamber about forty-eight hours. Since *Septoria* spreads only slightly in the dry atmosphere of the greenhouse and since celery is little affected by other pests under these conditions, this is a particularly convenient form for study. The difficulty of accurately measuring the amount of infection was obvious here as in all infection experiments. However, when only plants of equal age and approximately equal size are compared it seems accurate to count the total number of spots per leaf or per plant. This method is not satisfactory in older plants in variety tests since there is considerable difference in the size of mature plants of different varieties. The methods employed for the computation of leaf area are too unwieldy for use with plants in any considerable numbers.

NAME OF THE PARASITE

The specific name of the *Septoria* under consideration is involved in one of the more or less hopeless name tangles which serve so frequently to confuse the minds of botanical workers. Chester (4) in making one of the earliest reports (1891) on the

fungus in America expresses uncertainty as to the identity of the species but includes a description of the fungus and states that if it is a new species it "might be named *Septoria Apii*." Rostrup (33) in Denmark (1893) published the same name apparently independently. Briosi and Cavara (3) published their variety of *Septoria Petroselini* in 1890 (appeared 1891). Klebahn (17) reviewed the situation at some length, examined the exsiccati and decided in favor of the name *S. Apii* Rostr. Quanjer and Slagter in Holland (30) and Coons (8) in this country have treated the fungus under the same name. It will be noted later that the fungus I have studied, so far as it has been tested, does not produce infection on parsley either in the greenhouse or in the field. It has already been pointed out that no report of cross inoculations has been found in the literature, although a number of authors have taken it for granted that the form on parsley and the one on celery are identical. Therefore, whether or not it be granted that the failure to cross infect between these closely related hosts be considered ground for making a specific distinction, I shall continue to use the name *S. Apii* Rostr., especially since it is already quite widely distributed in the literature. The question of nomenclature may well be left till our knowledge of the life history of the fungus is completed by the discovery of an ascigerous stage.

CHARACTER OF THE SPOT

The spots on the celery leaves when mature are rounded, brownish, and usually quite distinct in outline. In severe cases, as the leaves become older and the spots more numerous, the tissue between the spots breaks down and the entire leaf may wither. Pycnidia may, however, appear while the spot is still quite or entirely green. In this respect *S. Apii* is widely removed from those species in which the pycnidia ripen after the development of a well-marked discolored area. The mycelium of the fungus is at first intercellular and may spread at least from one to two millimeters through the tissue before the cells of the host break down. This stage is reached after from ten to fifteen days, depending on the temperature, the condition of the host, and perhaps other factors. The collapse of the mesophyll and palisade cells is quite complete and leaves little more than the epidermal

layers with fragments of leaf cells mingled with the mycelium of the fungus making up the spot. Pycnidia begin to form before the tissue breaks down, in fact it is not uncommon, as has been noted, to see, with the hand lens, mature pycnidia with ostioles on tissue which is still green and in which no shrinkage can be detected. The pycnidium originates usually if not always in an intercellular space, frequently in the substomatal cavity and as it increases in size the adjacent cells are broken down and successively become replaced by the heavy thick-walled hyphal elements. Occasionally a portion of a cell may remain intact until its lumen is tightly packed with the mycelium. The origin of the pycnidium is not necessarily always subepidermal but may be at any point in the mesophyll or palisade tissue. On the petiole, however, the pycnidia seem to be restricted to the outer layers, none having been observed deeper than the third or fourth cell layer. When the leaf tissue collapses the pycnidia become more conspicuous, projecting above the general level of the spot. From the sharpness of the margin, which appears macroscopically between the spot and the surrounding tissue, it might be concluded that the margin of the mycelial growth is coincident or nearly so with the margin of the spot. In sections, however, the mycelium is found at a distance of several cell diameters in advance of the breaking down of the tissue. It has been noted further that pycnidia are visible with low magnification in the green margin surrounding the spot. As the spot ages, there is a reduction in the green color of the tissue immediately surrounding it. Strangely enough, however, when the leaf yellows from age this partially yellowed region retains its color longer than any other portion of the leaf. Whether or not the green is intensified in this area as it diminishes elsewhere, I am not able to say from my observations. However, it is plain that in some way the fungus has caused the prolongation of the life of the cells in this region beyond that of the cells of the remainder of the leaf. This is further evidenced by the fact that on petioles which are wilted gradually, the loss of both chlorophyll and water is inhibited in the vicinity of infected spots, especially the smaller spots (which do not lose any considerable amount of water through the dead tissue). This condition was especially marked in a plant in the field which had its lower roots cut by mice and was wilting slowly.

On the seed the fungus does not produce a definite spot. The pycnidium is found imbedded in the pericarp with only a small spreading of the mycelium into adjacent tissue. In the sections studied, the mycelium did not penetrate to the embryo. That this may occur, however, seems reasonably to be expected and it would probably result in most cases in inhibiting germination of the seed.

CULTURAL CHARACTERS OF THE FUNGUS

The fungus grows readily although slowly on a variety of media in pure culture. On starch,* beef peptone, and celery decoction agars the fungus produced somewhat greater radial growth at comparatively low temperatures (13°–19° C.) than at a temperature ranging from 22° to 27° C. On starch agar, which was the most satisfactory medium tested, a colony 15–18 mm. in diameter was produced in four weeks with mature pycnidia and considerable superficial fine white mycelium. As the culture ages the mycelium becomes coarser and darker until finally the surface of the medium is covered with a dense black weft. On the agar prepared from a decoction of celery leaves, the growth is similar to that described above but less vigorous. In marked contrast is the colony produced on ordinary beef peptone agar. The mycelium is dark and coarse from the beginning, radial growth is small and the result is an irregularly pulvinate colony very densely compacted. A somewhat similar growth was obtained on steamed coconut, bean stems, and petioles of celery and beet. When celery leaves were mixed with garden soil and steamed, no growth of the fungus could be obtained. Clean white sand was substituted for the soil and a good vigorous growth followed even spreading into the sand adjacent to the celery tissue.

SPECIALIZATION OF SEPTORIA APII AS TO HOSTS

It has been accepted by a number of pathologists in Europe, America and elsewhere that the *Septoria* of celery is transferable to parsley and *vice versa*, although I have found no record of inoculations to settle this question definitely. I have attempted to determne to what extent the celery fungus has become special-

* Czapek's formula, with 10 gm. corn starch substituted for the sugar.

ized in its choice of a host by inoculating plants from the following groups: (*a*) plants of the family Umbelliferae, including varieties of celery; (*b*) miscellaneous plants, nearly all of which are known to be hosts of *Septoria*. The varieties of celery were tested both in the greenhouse and in the field. TABLE I shows the relative

TABLE I

RELATIVE SUSCEPTIBILITY OF VARIETIES OF CELERY UNDER GREENHOUSE CONDITIONS*

Variety	No. of plants	Average number of spots per plant	
		First inoculation	Second inoculation
White Plume	12	15.7	170.5
New Rose	10	8.4	167.0
Golden Self Blanching	12	15.2	124.1
Giant Pascal	12	4.0	103.0
Winter Queen	12	2.4	51.4
Golden Half Dwarf	12	6.1	43.7
Celeriac	11	3.2	23.0

susceptibility of six of the common varieties of celery and of celeriac under greenhouse conditions. The plants grown in the greenhouse were six to eight inches high at the time of the first inoculation (June 26 and June 30), and were quite uniform in size (except the variety, Giant Pascal, which was somewhat larger). The plants were not in a vigorous growing condition judging from the yellowing of outer leaves and the slow rate of growth. It will be noted that the first inoculation produced comparatively low counts. The plants were inoculated again without repotting on August 27 and August 29 when conditions were more favorable for infection. The data as far as they go suggest that there is some consistent difference in varietal susceptibility, although no variety shows any pronounced resistance. The white varieties, Golden Self Blanching and White Plume, show especial susceptibility. In the field the variety test included the varieties Boston Market and Henderson's Easy Blanching, in addition to the varieties used in the greenhouse. The estimation of damage done by the fungus was much less simple in the field than in the

* A number of these plants were found to be infested by nematodes. However, among the lowest counts resulting from the infestation were those of three plants of the variety, White Plume, which stands highest in the total counts. Hence it does not seem that the presence of the nematodes materially affects the position of the varieties as presented here.

greenhouse. The season was favorable for vigorous development of the fungus and as a result the spots soon ran together and caused the collapse of the entire leaf. Consequently the method of counting spots could not be used. The total weight of celery produced would be inaccurate as an index of the severity of the attack, since the varieties differ normally in the weight of the mature plant. However, certain general conclusions can be drawn from the gross appearance of the plants at the end of the season. The plants were inoculated by atomizing a single plant of each variety on August 5. On October 29, at the time of digging, the variety Golden Self Blanching had been so severely damaged that only a few living leaves remained. During the latter part of the season while the plants were blanching, a soft rot was associated with the late blight on all of the varieties. This was especially severe on the Golden Self Blanching and seemed to follow in areas of dead tissue killed by the *Septoria*, especially on old leaves. The unusually wet period at that time would have favored the development of the various saprophytes which are present under such conditions. Of the varities other than Golden Self Blanching, there was no easily recognizable difference in susceptibility. Easy Blanching (Henderson's) seemed to withstand the blight and subsequent rot slightly better than the other varieties. White Plume, a self blanching form, was not noticeably poorer than the green varieties. An accurate method of estimating the amount of infection would probably have shown differences which could not be noted with certainty from the general appearance.

Infection tests on various Umbelliferae and a considerable number of miscellaneous plants have shown that the species of *Septoria* under consideration here is very limited in its host range, if not entirely restricted to the single species, *Apium graveolens*, and its variety *rapaceum*. Parsley (*Petroselinum sativum*) has been inoculated repeatedly in the greenhouse under controlled conditions but no sign of infection has been produced. The tests included the plain leaved parsley (two varieties), the curly-leaved type and the Hamburg or turnip-rooted parsley. The plain parsley was grown in the field in a row adjacent to heavily infected celery but infection was never found on any of the

plants. Whether there are other strains of the fungus which infect both celery and parsley is a question of interest, both theoretically and practically, and should receive further attention. The various other hosts tested were grown in pots in the greenhouse and inoculated with celery plants in every case to check on the conditions for infection. The following plants were tested:

UMBELLIFERAE

Anethum graveolens L., dill
Anthriscus cerefolium (L) Hoffm., chervil (beaked parsley)
Carum Carvi L., caraway
Coriandrum sativum L., coriander
Cryptotaenia canadensis (L.) DC., hone wort
Daucus Carota L., carrot (both wild and cultivated)
Foeniculum officinale All., fennel
Osmorhiza sp., sweet cicely
Pastinaca sativa L., parsnip
Petroselinum sativum Hoffm., parsley (plain leaf, curly leaf, and Hamburg varieties)
Silaus Besseri

MISCELLANEOUS

Antirrhinum majus L., snapdragon
Beta vulgaris L., beet (sugar and garden varieties)
Lactuca sativa L., lettuce
Lobelia sp.
Lycopersicum esculentum Mill., tomato
Nicotiana Tabacum L., tobacco
Pisum sativum L., pea

None of the plants listed here developed any sign of infection. From these data it must be concluded that the *Septoria* of celery has reached a comparatively high degree of specialization as to its hosts. These results agree essentially with those of Beach (1), working with a considerable number of other species of the genus *Septoria*.

EFFECT OF FERTILIZERS UPON INFECTION

Realizing that the terms health, vigor, and vitality are vague and difficult of definition in plants as in animals, I have attempted

to modify these conditions in celery plants by various methods of feeding and handling to determine the influence of such treatment upon the interaction of host and parasite. The direct effect upon the plants has been visible in some cases in the increase or decrease in growth, the putting out of new leaves or the dropping of old leaves and in the turgidity of the tissues. In other instances the reaction to the treatment was not so directly evidenced. The difficulty in obtaining properly controlled results is obvious, but I have made a number of experiments to test the amount and character of the infection produced by inoculating plants in different conditions of health more or less artificially induced.

One of the first striking results noted was that which was produced by treating pot bound plants with sodium nitrate in solution. Five plants in four-inch pots of garden soil received each 1 gram of sodium nitrate in 100 c.c. of water. In this and in the succeeding experiments, the control plants received an amount of water equivalent to that used in the solution with the nutrient. The plants were inoculated at the time the nitrate solution was added.

TABLE II

INCREASE IN INFECTION PRODUCED BY TREATING POT BOUND PLANTS WITH SODIUM NITRATE SOLUTION

Plant No.	1	2	3	4	5	Average No. leaves	Average No. spots per leaf
Sodium nitrate.....	348	185	177	189	238	10.6	24.3
Control.....	234	97	11	43	38	8.0	10.6

TABLE II shows the very marked increase in infection obtained upon the plants which received the fertilizer. This difference is unusually marked due to the fact that the plants were badly pot bound and growth had been markedly checked.

With the garden soil used, the addition of calcium sulfate in the dry form, as it has been used in agricultural practice, produced a small decrease in infection. This series was prepared by mixing about five grams of calcium sulfate with the soil of each pot at the time of repotting. Twenty-four days later these plants were inoculated with controls. After the records were taken these plants were kept upon the greenhouse bench in compara-

tively dry atmosphere until the infection had largely been thrown off. They were again inoculated July 10, nine weeks after the first inoculation. The results of both inoculations are shown in TABLE III. The lower counts on the second inoculation may be

TABLE III

DECREASE IN INFECTION UPON PLANTS TREATED WITH CALCIUM SULFATE

Plant No.	First inoculation						Second inoculation						Spots per plant, first inoculation	Spots per plant, second inoculation
	1	2	3	4	5	6	1	2	3	4	5	6		
$CaSO_4$	387	281	266	301	271	505	87	28	56	14	80	79	335.1	57.3
Controls	623	368	495	350	342	382	94	113	172	99	80	36	426.6	99.0

explained partly by the fact that the plants had by this time become pot bound and partly by the influence of seasonal conditions, for during the warm weather of midsummer, no high infection counts were obtained on any plants in the greenhouse regardless of their condition. It will be seen that there is a consistent decrease in the counts on the treated plants from both inoculations. The plants were not appreciably altered in appearance by this application.

TABLE IV

EFFECT UPON INFECTION OF FEEDING WITH VARIOUS FERTILIZERS AND IN ONE CASE TOP DRESSING WITH LIME

Plant No.	1	2	3	4	5	6	7	8	9	10	Average No. leaves	Average No. spots per leaf
Controls	246	607	168	143	614	799	460	1,139	589	196	6.0	82.6
KH_2PO_4	506	412	778	318	385	925	1,117	592	144	362	6.5	85.2
$Ca(NO_3)_2$ and KNO_3	412	429	723	286	779	982	645	748	260	376	6.3	89.5
Complete nutrient solution	559	662	1,237	276	1,009	1,242	543	403	247	429	6.9	95.7
Sheep manure	494	772	461	576	522						5.0	113.0
Hydrated lime ($CaCO_3$)	103	259	518	394	430						5.6	60.8

With these results in mind further tests were planned to include complete fertilizers as well as their components. A nutrient solution was prepared according to a Pfeffer formula (27): 4 gm. calcium nitrate, 1 gm. potassium nitrate, 1 gm. magnesium sulfate, 1 gm. potassium acid phosphate, 0.5 gm potassium chloride, trace of ferric chloride, were dissolved in 3 liters of water.

Ten plants received each 100 c.c. of this solution. Two other sets of ten plants were treated respectively with nitrates and phosphates equivalent to the amounts fed to the first set in the complete nutrient solution. Five plants received 5 gm. each of hydrated lime on the surface of the soil and the soil of five others was top dressed with sheep manure. All of these plants were inoculated together with controls immediately after the addition of the fertilizers. The infection counts from them are shown in TABLE IV. All of the plants seemed vigorous in their gross appearance except those treated with lime. In this case the roots in the upper inch or so of the soil were discolored and some appeared to be killed outright. The leaves appeared somewhat less turgid and vigorous than those of the other series.

The small margin of difference between the controls and treated plants, especially in the case of the phosphate, makes the results appear doubtful. It must be borne in mind, however, that the concentration of the solutions was that recommended for water cultures and did not result in marked increase of growth in the treated series. When it is considered that each plant in the nitrates series receives only 0.166 gm. of the salt, it will be seen that striking results cannot be expected except with the lime and manure whch were applied in considerable quantity. However, the results are in accord with those of the other experiments reported here. Whether or not the increase in new growth under field conditions would enable fertilized plants to increase the total yield in spite of increased infection is of course not shown by these experiments.

In watching the plants from day to day it seemed that not only was there an increase in the number of spots on plants treated with fertilizer but there was also a tendency toward the formation of larger spots and more rapid breaking down of the tissue between the spots. In the field, where conditions were more favorable for the growth of the host than could be supplied in pots in the greenhouse, a count of our nineteen hundred spots was obtained from a single leaf (Easy Blanching) and, as will be pointed out later, the older leaves regularly withered entirely from the coalescing of the spots. It is true that the field conditions of the season in question were also more favorable for the develop-

ment of the fungus than the greenhouse conditions. However, the fact that a single leaf in the field bears more infections than any count obtained on an entire plant in the greenhouse is noteworthy. To obtain some statistical evidence of the relation of the fertilizer treatments to the size of the spot, two sets of five plants each in three-inch pots were treated respectively with 2 grams of hydrated lime per plant as top dressing, and 1 gram of sodium nitrate per plant in solution. The effect upon both the number and extent of infection areas is shown in TABLE V.

The nitrate plants average 284 spots per plant as opposed to 120 spots per plant on the limed plants and, what is perhaps even more significant, the difference in the size of the spots is proportional, the spots of the nitrate plants averaging 2.64 mm. in diameter while those of the limed plants average only 1.06 mm. The ratios are as 1: 2.36 and 1: 2.54, respectively. These data indicate that the degree of susceptibility is dependent upon the interchanges between the host cells and fungus hyphae rather than upon the ability or lack of ability of the fungus to penetrate the host.

In a further attempt to produce varying conditions of health in the experimental plants, sets of five plants each were watered with 50 c.c. of each of the following solutions: 2 per cent sodium chloride, 1 per cent magnesium chloride, 1 per cent barium chloride, 0.1 per cent ferric chloride, 0.1 per cent zinc chloride. These were inoculated with controls as in the preceding experiments. The results are not sufficiently uniform to be considered significant. The health and growth of the plants were not perceptibly altered and the amount of infection was fluctuating. The plants treated with magnesium, iron and zinc were somewhat lower in total counts than the controls, while the barium series gave the highest counts of all. It is to be remembered that our lack of knowedge in regard to the behavior of these substances in relation to the soil and to the selective absorption phenomena exhibited by the roots of plants would make any but the most striking results extremely difficult of interpretation.

Bearing upon the question of the relation of fertilizers to infection is the following experiment, which was begun with other matters in view. Five five-inch pots were filled about one-third

TABLE V

COMPARISON OF THE NUMBER AND SI-E OF SPOTS ON PLANTS TREATED WITH SODIUM NITRATE AND HYDRATED LIME. NOTES TAKEN TWENTY DAYS AFTER INOCULATION

Treatment	Plant No.	Leaf No.	Diameter of spots in millimeters										Aver.	No. spots per plant	No. leaves per plant
			1	2	3	4	5	6	7	8	9	10			
Hydrated lime	1	1	0.5	0.5	0.5	0.5	0.5	0.5	1.0	0.5	1.0	0.5	0.60	113	5
		2	1.0	0.5	0.5	0.5	0.5	0.5	1.0	0.5	0.5	0.5	0.60		
		3	0.5	0.5	1.0	0.5	0.5	0.5	0.5	1.0	0.5	0.5	0.60		
	2	1	5.0	3.0	5.0	3.0	3.5	3.0	3.0	5.0	6.0	4.0	3.95	159	6
		2	2.5	2.0	1.0	1.0	2.0	1.0	2.0	1.5	1.0	1.0	1.50		
		3	3.0	2.0	1.0	0.5	1.0	0.5	1.5	1.0	0.5	0.5	1.15		
		4	0.5	1.5	1.0	0.5	1.0	0.5	1.0	1.0	0.5	1.0	0.85		
		5	0.5	1.0	0.5	0.5	0.5	0.5	0.5	1.0	0.5		0.61		
	3	1	1.5	1.0	1.5	2.0	4.0	1.0	0.5	1.0	3.0	1.0	1.65	159	6
		2	1.0	1.0	1.0	1.0	0.5	0.5	1.0	0.5	0.5	2.0	0.90		
		3	1.0	0.5	1.0	1.0	0.5	0.5	1.0	0.5	0.5	1.0	0.75		
	4	1	0.5	1.0	0.5	1.0	0.5	1.0	1.5	1.0	1.0	0.5	0.85	135	5
		2	1.0	1.5	0.5	0.5	1.0	0.5	1.0	0.5	1.0	1.0	0.85		
		3	0.5	1.0	0.5	1.0	1.0	0.5	1.0	1.5	0.5	1.0	0.85		
	5	1	1.0	1.5	1.0	0.5	1.0	0.5	0.5	1.0	0.5	1.0	0.85	36	6
		2	0.5	0.5	0.5								0.50		
		3	1.0	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	1.0	0.60		
Sodium nitrate	1	1	3.0	2.5	5.0	4.0	6.0	4.0	3.0	4.0	4.0	7.0	4.25	459	7
		2	5.0	5.0	5.0	5.0	5.0	6.0	5.0	6.0	7.0	6.0	5.40		
		3	4.0	3.0	3.0	5.0	1.0	3.0	3.0	1.5	3.0	3.0	2.95		
		4	2.0	2.0	1.0	1.0	1.0	1.5	2.0	1.5	1.5	2.0	1.55		
	2	1	7.0	6.0	5.0	6.0	6.0	6.0	6.0	7.0	5.0	5.0	5.90	314	8
		2	3.0	4.0	5.0	4.0	5.0	4.0	2.0	3.0	3.0	3.0	3.60		
		3	3.0	5.0	7.0	4.0	5.0	2.5	4.0	1.5	2.5	5.0	3.95		
		4	2.0	4.0	3.0	1.0	3.0	4.0	3.0	3.0	4.0	2.5	2.95		
		5	2.0	1.0	2.0	1.5	1.5	2.0	2.5	1.0	2.0	1.5	1.70		
	3	1	2.0	3.0	2.0	3.0	3.0	1.5	1.0	2.0	2.0	1.0	2.05	177	9
		2	1.5	1.0	1.5	2.0	1.0	1.5	1.0	1.0	1.0	1.0	1.15		
		3	1.5	0.5	1.0	1.0	0.5	1.0	1.0	1.0	3.0		1.16		
	4	1	5.0	2.0	1.0	2.5	3.5						2.80	145	10
		2	1.5	6.0	3.0	1.5	4.0	2.0	4.0	1.0	3.0	1.0	2.70		
		3	2.0	2.0	3.0	4.0	2.5	3.5	2.0	1.0	2.0	4.0	2.60		
		4	3.0	3.5	2.0	2.0	3.0	2.0	3.0	3.0	1.5	1.0	2.40		
		5	1.0	0.5	0.5	3.0	2.0	1.0	0.5	1.0	0.5	1.0	1.10		
		6	0.5	0.5	1.0	1.5	1.5	1.0	0.5	0.5	1.5	1.0	1.05		
	5	1	2.0	3.5	3.5	3.0	1.0	1.0	0.5	1.0	0.5	3.0	1.90	325	7
		2	3.0	3.0	2.0	2.0	4.0	1.0	3.0	1.0	2.5	2.5	2.40		
		3	1.0	1.0	2.0	2.0	2.0	2.0	2.5	3.0	3.5	2.0	2.10		
		4	1.0	0.5	0.5	0.5	2.0	0.5	1.0	0.5	0.5	1.0	0.85		

full with heavily diseased leaves and petioles of celery. Five pots were similarly filled with healthy green leaves. Celery plants were potted in garden soil in the upper part of these pots and twenty days later these plants were inoculated. The result was a very decided increase in infection upon the plants which received the diseased material (TABLE VI). While there was no perceptible

TABLE VI

INFECTION ON PLANTS TREATED WITH DISEASED CELERY LEAVES IN THE SOIL

Plant No.		1	2	3	4	5	Average No. spots per leaf
Plants with diseased material	Spots per plant.....	260	288	372	361	153	38.7
	Leaves per plant...	9	7	6	9	6	
Controls	Spots per plant.....	159	217	255	132	187	19.7
	Leaves per plant...	13	7	13	8	7	

difference in the appearance of the two series of plants, the most reasonable explanation of these results is that the diseased material with decay already under way would supply, at the time of inoculation, a condition similar to that produced by the application of manure made in an earlier experiment. The depth at which the material was buried and the uniformity in time with which the infection appeared preclude the possibility of the action of this material as an additional source of inoculum.

INFECTION OF PLANTS INFESTED BY NEMATODES

Perhaps the most conclusive data bearing on the relation of health to infection were obtained incidentally in the course of experiments planned for other purposes. Twelve plants which had received various treatments were given two successive inoculations, which produced at most only a few spots. These were finally thrown out and the roots were found to be heavily infested by nematodes. Again nine plants were set aside from a variety test as possibly resistant individuals. These were also found to be infested. The infection (*Septoria*) on these plants is compared with that on two non-infested plants of the same experiment in TABLE VII. So far as these observations extend, nematodes do not develop to any marked degree on any except badly pot-bound plants. However, a number of galls may be produced on the roots of plants in fairly good growing condition. A number

TABLE VII

REDUCTION IN NUMBER OF SPOTS PRODUCED BY SEPTORIA ON PLANTS INFESTED BY NEMATODES

Variety	Infested by nematodes									Not infested	
	Winter Queen	Winter Queen	Winter Queen	White Plume	White Plume	New Rose	Golden Half Dwarf	Golden Half Dwarf	Golden Half Dwarf	New Rose	Golden Self Planching
No. of leaves	5	4	5	5	5	5	5	7	4	4	4
Spots per plant	15	8	5	56	19	12	19	5	29	503	385

of these cases were noted in connection with the fertilizer experiments previously described, in which no reduction in vigor of the plant or in the amount of infection could be detected. An attempt to produce the infestation by inoculation into the soil was made with ten young plants in good growing condition but at the end of ten weeks, no galls were evident. The history of a single plant which has been followed more closely will throw light on the rôle which the nematode plays here. A plant was noted as "highly resistant" in the course of an experiment and when reinoculated it had lost its susceptibility completely. The roots were very heavily infested by nematodes. The plant was placed in a larger pot with fresh soil and five weeks later, when considerable growth had been made, it was again inoculated with a control. At the end of twenty-eight days no spot recognizable as due to *Septoria* could be found on the plant. The control plant bore 219 spots. Seven weeks after this inoculation the "nematode" plant was treated with 300 c.c. of the nutrient solution described above with the fertilizer experiments. At this time a few small spots could be seen with an occasional pycnidium. The plant was finally inoculated six days after the addition of the fertilizer and thirty days later a count of 478 spots was obtained. These spots were for the most part small and the fructification of the fungus was feeble. According to the accounts of the behavior of nematodes in the roots of plants, it seems clear that the foliage is starved both by the disruption of the vascular elements and by the withdrawal of food materials to produce the galls. Here is undoubtedly a clear case of the reduction of infection by a fungus parasite running parallel with the reduction in vigor of the host.

INFECTION OF ETIOLATED PLANTS

The effect of etiolation of the host upon infection has been tested in various ways. The first series of plants were kept in a dark room for nine days just preceding inoculation. Controls were kept on the greenhouse benches. The counts of spots per plant are shown in TABLE VIII. This prolonged period in the

TABLE VIII

EFFECT UPON INFECTION PRODUCED BY ETIOLATING PLANTS FOR NINE DAYS IMMEDIATELY PRECEDING INOCULATION

Plant No.	1	2	3	4	5	6	Total No. leaves	Average No. spots per leaf
Etiolated	62	172	29	63	35	39	50	8.0
Control	33	40	312	253	400	72	64	16.7

total absence of light materially changed the plants in a number of ways. The most noticeable changes were loss of chlorophyll, elongation of the petiole, and reduction in size of the leaflets. The reduction in leaf area, however, was plainly not commensurate with the difference in amount of infection. Neither can the suspension of photosynthesis be held entirely accountable for the less vigorous action of the parasite, in view of the various other changes in the host and in the light of the following further experiments.

The second series of plants were kept in the dark room for three and one half days immediately following their removal from the inoculation chamber. The plants were not materially changed in appearance and it may be seen at once in TABLE IX that no

TABLE IX

EFFECT OF ETIOLATION FOR THREE AND ONE-HALF DAYS FOLLOWING THE REMOVAL OF PLANTS FROM THE INCUBATION CHAMBER

Plant No.	1	2	3	4	5	6	Total No. leaves	Average No. spots per leaf
Etiolated	422	163	313	584	403	565	48	50.9
Control	623	368	495	350	342	382	47	54.4

noteworthy variation was produced in the amount of infection as compared with the control plants. It was noted moreover

that the time* required for the first appearance of the spots was practically identical for the etiolated and control plants.

A third set of plants was kept in the dark room for five days, beginning on the thirteenth day after inoculation, at which time the spots were just beginning to appear. This dark room was provided with a ventilator which caused a continuous circulation of air from the greenhouse in which the control plants were kept thus providing similar atmospheric conditions for the two sets of plants. This experiment was performed during the warm weather of July, and as a result the plants kept in the dark room lost several of the older leaves. Although the total counts of infections could not be obtained it is scarcely to be expected that the number of spots would be altered by this treatment.

TABLE X

EFFECT ON SIZE OF SPOT OF ETIOLATION AT DIFFERENT TIMES RELATIVE TO INOCULATION

a. Plants kept in dark room nine days preceding inoculation

Plant No.	Etiolated plants		Control plants	
	Average size spot	No. of leaves	Average size spot	No. of leaves
1	1.62	5	1.17	6
2	1.51	5	1.16	9
3	1.37	4	0.91	4
4	1.54	3	0.95	8
5	1.45	3	0.94	4
b. Plants kept in the dark room from the fifteenth to the eighteenth day after inoculation				
1	2.08	3	1.27	2
2	1.87	2	1.51	4
3	1.50	2	1.07	5
4	1.80	1	1.81	3
5	1.75	2	1.45	3
6	1.78	3	1.33	3

This seemed to be borne out by counts from the individual leaves. The effect upon the size of the spot produced by etiolation at this time was readily demonstrable. TABLE X shows the increase in diameter of spots upon plants etiolated both before and after inoculation. Except for an occasional leaf (nine altogether)

* Fromme found (12) that *Puccinia coronifera* on oats was almost completely arrested in its progress during the time in which inoculated plants were kept in the dark room.

ten spots per leaf were measured. Thus for a plant of five leaves fifty spots were measured.

In the case of the first series kept in the dark room before inoculation, the most marked increase in the size of the spots was on the youngest leaves, which were put out partly or entirely while the plants were in the dark room. On these the spots at times exceeded in diameter those on the oldest leaves. In the last series of plants the increase in size apppeared to be proportionate for all the spots. It has been noted that when infected plants are placed in the inoculation chamber, for forty-eight hours, a zone of at least one half to one millimeter surrounding each spot is broken down. That the mycelium of *Septoria* should advance this distance in so short a time does not seem probable. It appears rather that the weakened tissues of the host plant succumb where the fungus is already present.

RELATION OF TEMPERATURE TO INFECTION

It has been recognized since the late blight disease began to be studied that it is more severe in the early autumn than during mid-summer. I have found this to be true in the greenhouse as well as in the field. Several experiments have been performed to test the relation of this condition to temperature. Plants were inoculated uniformly and divided into two groups which were kept through part or all of the incubation period at temperatures

TABLE XI

EFFECT OF MAINTAINING INOCULATED PLANTS AT DIFFERENT TEMPERATURES THROUGHOUT THE INCUBATION PERIOD OF TWENTY-ONE DAYS

Mean av. temperature	Number of infections per plant										
	1	2	3	4	5	6	7	8	9	10	Average
21.9° C.	383	272	327	281	189	377	98	133	209	269	253.7
13.3° C.	144	86	120	52	3	64	111	73	104	37	79.4

differing from 7 to 13 degrees Centigrade (mean average). Five sets of from ten to twenty plants each were inoculated. The infection develops more rapidly at higher temperatures but later counts show usually no striking difference and the individual plants vary widely. One set (TABLE XI) showed a marked though not altogether consistent difference in counts. However,

a second record five days after the first showed an average increase of fifteen spots per plant on the plants of the lower temperture. One set of plants showed a consideraby higher count on the plants of lower temperature after thirty-six days. The results are too variable to be in any way conclusive. A factor of probably greater importance is the fact that the host plant may be more vigorous and make its greatest growth in cool weather with the autumn rains. Rolfs (**32**) states that in Florida celery can be grown only as a cool weather crop. Lloyd (**20**) and Watts (**41**) point out that celery demands cool weather, at least cool nghts, for satisfactory growth. However, I have not found any specific data to show the optimum temperature for the culture of celery.

RELATION OF AGE TISSUE TO INFECTION

The absence of any conspicuous sign of infection in the field during the early and middle parts of the growing season led the earlier workers to believe that young plants were affected only slightly or not at all. The more careful observations of later workers have already disproved this. I have observed the fungus on plants in the various stages from the seed bed to maturity.

TABLE XII

NUMBER OF SPOTS ON LEAVES OF DIFFERENT AGES TWENTY-SEVEN DAYS AFTER INOCULATION

Leaf No.*	1	2	3	4	5	6	7	8	9	10
Plant No. 1	0	0	18	209	254	75	17	50		
" 2	0	0	35	193	61	79				
" 3	0	0	5	93	185	127	44	41		
" 4	0	0	0	40	95	136	26	25	24	4
" 5	0	0	52	216	36	27	11			
" 6	0	0	39	194	42	67	31	9		
Totals	0	0	149	945	673	511	129	125	24	4

In the field a row of young plants was set out on July 17 so that they were about half grown when the infection was becoming severe on the regular crop (late September). Counting the number of spots per leaf is not practicable under field conditions but it was obvious that these young plants were attacked with a severity quite sufficient to throw doubt on the idea of a close

* The leaves are numbered here from the center of root crown outward, i.e., from youngest to oldest.

TABLE XIII

SIZE OF SPOT (DIAMETER IN MILLIMETERS), AS AFFECTED BY AGE OF THE LEAF. THESE SPOTS WERE MEASURED ON THE BASAL LEAFLET PAIR OF EACH LEAF NINETEEN DAYS AFTER INOCULATION. LEAF NO. 1 IS THE OLDEST

Spot No.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	Average	No. of spots	Condition of leaf
Leaf No. 1....	1.0	2.0	2.0	3.0	3.0	2.0	2.0	2.0	1.5	1.5	2.0	1.5	5.0	4.0	2.5	2.0	3.0	2.0	1.0	2.0	2.0	2.0	3.0	2.5	2.0	2.26	159	Yellowed, drying
" 2....	1.5	1.5	1.0	1.0	1.0	1.5	2.0	1.5	1.5	1.0	1.0	0.5	1.0	0.5	1.5	1.5	1.5	2.5	2.0	1.0	1.0	2.5	0.5	1.0	2 0	1.34	305	Yellowing
" 3....	1.0	1.5	1.5	2.0	2.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	0.5	1.5	2.0	0.5	2.5	2.0	1.0	1.0	1.0	1.5	1.30	379	Yellowing slightly
" 4....	2.0	1.5	1.5	1.0	1.0	1.0	1.0	1.0	1.5	2.5	1.0	1.0	1.5	1.5	2.0	2.0	2.0	0.5	1.0	1.0	0.5	2.0	1.5	1.5	0.5	1.34	212	Green
" 5....	1.0	0.5	1.0	1.5	1.0	1.0	0.5	0.5	0.5	0.5	1.0	1.0	0.5	1.0	0.5	1.0	2.5	1.0	0.5	1.0	1.0	1.5	1.0	1.0	1.0	0.94	209	"
" 6....	1.0	1.0	0.5	0.5	.05	0.5	0.5	0.5	1.0	1.0	0.5	0.5	1.5	1.0	1.0	0.5	1.0	0.5	1.0	0.5	1.0	0.5	1.0	1.0	0.5	0.76	114	"
" 7....	0.5	0.5	1.0	1.0	1.5	1.0	1.0	0.5	0.5	0.5	0.5	0.5	0.5	0.5	1.0	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	1.0	1.0	0.68	90	"

relation between the age of the plant and its susceptibility. However, as regards the relative susceptibility of leaves of different ages on the same plant, results have been obtained to show that there is a definite and constant relation between the age of the leaf and the number of spots produced by inoculation (TABLE XII).

The leaves which show no infection are those which were pushed out after the inoculation was made. It has been determined by tagging the young leaves at the time of inoculation that a leaf is susceptible as soon as it pushes out into view. It does not however unfold the leaflets so as to be exposed to the inoculum on all its surface until it has reached a height of from two to four inches. This accounts in part for the smaller count on the very young leaves. No method has been devised to determine whether or not these leaves are as susceptible per unit area as leaves which have completely unfolded. The chief point of interest here is that a very much larger number of infections is established on leaves which are still actively growing than on leaves which are more mature. Another very interesting difference in the behavior of leaves

of different ages in relation to fungus invasion is found in the rate of breaking down of the leaf tissue after infection becomes established. Except in unusual cases in the greenhouse there was little coalescing of spots until some days after the infection was evident on all of the leaves. Thus time was allowed for measurement of the size of spots even on very old leaves while they were still distinct in outline. It was found that for a given distance between spots, the older the leaf the more rapidly the intervening tissue breaks down.

TABLE XIII shows the diameter measured to the nearest half millimeter of twenty-five spots on each leaf of a plant nineteen days after inoculation. The marked decrease in the size of the spots from the oldest to the youngest leaf is at once apparent.

In TABLE XIV the averages are shown for a number of other plants which were similarly studied. It has been pointed out that the margin of the killed area produced by *Septoria* is not identical with the limit of mycelial spread. Whether or not the fungus colony exceeds the margin of the spot as far in old leaves as in young leaves has not been determined.

TABLE XIV

AVERAGE SIZE OF SPOTS ON LEAVES OF THE SAME PLANT AT DIFFERENT AGES.

Leaf No.	1	2	3	4	5	6	7	8	9	No. spots measured*	Age of infection
Plant No. 1....	2.18	1.22	0.94	0.72	0.64					25.0	19 days
" 2....	1.32	0.88	0.74	0.74						25.0	19 "
" 3....	1.66	1.06	0.86	0.80	0.58					25.0	19 "
" 4....	1.30	1.10	1.00	0.55						10.0	29 "
" 5....	1.45	0.70	0.70	0.70						10.0	29 "
" 6....	1.80	1.40	1.25	1.20	0.80	0.60				10.0	29 "
" 7....	1.30	1.35	1.15	0.70	0.90	0.75	.77	.62		10.0	29 "
" 8....	2.05	2.00	1.20	1.00	0.95	0.95	.80	.75	.75	10.0	29 "

A possible relation between the acidity of plant juices and their susceptibility to fungus attack has been claimed by Comes (6). With this in mind two lots of leaves were collected from a number of celery plants, the oldest being included in one lot and the youngest in another. These were put through a meat grinder and 15 gram samples of each were extracted for thirty minutes in 200 cc. distilled water. The extracts were filtered and 100 cc. of the filtrate were titrated against approximately twentieth normal

* In four leaves less than the number of spots indicated was used.

sodium hydrate solution. A very marked increase in acidity was thus shown for the old leaves. The ratio of the readings for young and old leaves was 4.6 : 6.3.

Sorauer (**36**) states that acidity is higher in etiolated plants than in the normal green. It has been pointed out that young leaves developed in the dark room bear spots as large as those produced on very old leaves. This suggests the possibility of a relation between the size of the spot and the acid content of the leaf. Obviously, however, no more than a suggestion can be made from the data at hand.

DISCUSSION

The relations of host and parasite are apparently as different for the groups of saprophyte, semi-saprophyte, and obligate parasite as are the modes of life of the organisms. It is possible to arrange an intergrading series according to the completeness of adaptation to the host, from a form such as *Botrytis* (see Blackman and Welsford, **2**), which habitually kills the host cells before it reaches them and is probably never in intimate contact with the living cell, to a form such as the seed fungus of *Lolium temulentum* (see Freeman, **11**), which has reached such a high degree of adjustment with the host that it is perpetuated entirely in the mycelial form through the seed of the host and perhaps never kills any of the host cells. As the adaptation to the host becomes more nearly complete, there is an increasing tendency to show some of the features of mutualism and symbiosis. Fromme (**13**) has observed with the angular leaf spot of tobacco and Peltier (**25**) with citrus canker that infection is heavier under conditions which favor the growth of the host. Marchal (**21**) found that infection of lettuce by *Bremia Lactucae* was favored by nitrogen and phosphates and retarded by an excess of potash. The experiments described in this paper show that *Septoria Apii*, although it readily assumes the saprophytic habit, has become so adapted to its host that the development of infection is favored by increased growth in the host, such as is produced by feeding the plants with nitrates, with a complete nutrient solution, or by top dressing the soil with sheep manure. The acceleration is manifested in both the number of infections

established and the size of the spots produced. On the other hand top dressing the soil of pots with lime decreases the infection. Also the infestation of the roots of celery plants by nematodes partially or entirely inhibits the development of the fungus. The retention of chlorophyll and water in the tissue adjacent to infected spots after these have disappeared from the remainder of the leaf is further evidence of a tendency toward mutualism between the fungus and host. McCue (**22**) observed that tomato plants treated with phosphatic fertilizers developed less leaf blight (presumably *Septoria*) than control plants, while those on nitrogen and potash plots were more heavily infected than the controls. At the same time the highest yields (showing greatest vigor of growth), were obtained from the plants which received nitrogen and potash. Norton (**24**) also noted a decrease in infection by *Septoria* on tomatoes treated with phosphates.

Cereals grown by Spinks (**37**) in nutrient solution seemed to be susceptible to infection by *Erysiphe* in proportion as vigorous growth of the host was maintained. Excess of phosphates and potash diminished susceptibility while nitrates increased it. Stakman (**38**) noted that heavy manuring of rye increased the number of successful inoculations with *Puccinia graminis Avenae*. Even the seed fungus, however, is surpassed in some mutualistic characters by the mycorrhizas and lichens. The mycorrhizas show grades of interrelation between host and parasite from active parasitism to finely adjusted mutualism. Stout (**39**) has shown that *Sclerotium rhizodes* may be parasitic on aerial parts of *Calamagrostis canadensis* and at the same time assume a mycorrhizal habit on the roots of the same host. Nieuberg (**23**) found that in the lichens mutualism persists for a long period perhaps even after the fungus finally penetrates the algal cells. This habit is a close approach to that of producing haustoria as in the more specialized parasites.

With the exception of the nitrogen fixing bacteria, only the mycorrhizal and lichen fungi have been proven to contribute anything of value to the host. It is important, however, in the development of methods of avoiding disease in plants, as well as for a clearer understanding of the nature of parasitism, that it be recognized that the relation of host and parasite is not of necessity

antagonistic throughout but may on the contrary become specialized in such a way that infection and the development of the typical symptoms of the disease are directly favored by the general vigor of the host plant.

In the relation of the age of different tissue on the same celery plant to infection, it seems that there are two entirely separate conditions operating, one which governs the establishment of infection and another which determines the rate of subsequent spread of the mycelium. The first stage seems closely related to the immediate metabolic activity of the host cells especially in view of the marked increase in the number of infections produced by the addition of fertilizers to the plant at the time of inoculation. That starch metabolism has no very direct relation to infection is indicated by the results of inoculating etiolated plants.

Pool and McKay (**28**) state that the infection of *Beta vulgaris* by *Cercospora beticola* is closely related to, if not directly controlled by the movement of the stomata. According to their data (pp. 1019, 1031), however, heart leaves which are said not to be infected show an average stomatal pore width of from 0 μ to 9 μ between 10 A.M. and 1 P.M., only one case in ten falling below 2.5 μ. Celery leaves can be infected as soon as they come into view but they frequently reach their mature height before the spots are visible. It is not clear whether the incubation period is taken into consideration in this connection by Pool and McKay. They do not show comparative counts on old and young leaves from a single infection. These authors show a close correlation between the maturity of the leaf and the number of stomata per unit area. Ensign (**10***a*) has shown a very definite relation between the size of the vein-islets and maturity of the leaf in citrus. The relation of infection to age of the host as determined by these criteria deserves further attention.

It has been pointed out that the tissue between spots separated by a given distance will break down more rapidly on old leaves than on young ones. It has been noted furthermore that from a single inoculation the spots are visible on the old leaves one to several days before they can be seen on the younger leaves.

The *Septoria* produces a vigorous growth on widely different culture media, as well as on cooked celery, but at the same time

is unable to develop on a living host as nearly related to celery as is parsley.

The comparatively narrow specialization of the *Septoria* on celery suggests a promising outlook for experiments in breeding for resistance. More intensive work in this direction is needed.

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DEPARTMENT OF BOTANY
COLUMBIA UNIVERSITY

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